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Evolution

Early Cretaceous mammal from North America and the evolution of marsupial dental characters

(vertebrate paleontology/biogeography/Tribosphenida/Metatheria)

RICHARD L. CIFELLI

Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, OK 73019

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ABSTRACT **A mammal from the Early Cretaceous of the western United States, represented by a lower jaw exceptional in its completeness, presents unambiguous evidence of postcanine dental formula in an Early Cretaceous marsupial-like mammal, and prompts a reconsideration of the early evolution of marsupial dental characters. A marsupial postcanine dental formula (three premolars and four molars) and several marsupial-like features of the lower molars are present in the new taxon, but a hallmark specialization of marsupials (twinning of the hypoconulid and entoconid on lower molars) is lacking. This, coupled with recent evidence from the Late Cretaceous of the western United States, suggests that the distinctive marsupial dental formula evolved prior to the most characteristic specialization of lower molars and that apomorphies presumed to be diagnostic of the upper molars (such as auxiliary stylar cusps) were relatively more recent developments in marsupial history. Dental evidence supports the monophyly of higher (tribosphenic) mammals and suggests that the predominantly Old World Deltatheroida, recently proposed as a sister taxon to marsupials, represents a primitive and unrelated group of higher mammals; by this interpretation, early marsupials and their presumed close relatives are restricted to North America. This, together with the hypothesized relationships of South American/Australian marsupials (in the context of the North American Cretaceous radiation) and evidence from the fossil record of South America, in turn supports a North American origin for the group.**

Although the initial diversification of tribosphenic mammals [marsupials, placentals, and presumed allies, termed Theria of metatherian–eutherian grade (1) or tribotheres (2)] took place in the Late Jurassic or Early Cretaceous (3), very little is known from that time period. The most fundamental differences between the living groups, marsupials and eutherians, lie in the reproductive system (4) but, because of the nature of the fossil record, systematists have long relied heavily on characteristics of individual molar teeth in interpreting the dynamics of the earliest radiation of higher mammals (2, 5, 6). The specimen described below, the most complete known (in terms of number of tooth loci represented) from the Early Cretaceous, was collected at a newly discovered and highly productive vertebrate microsite in the Cedar Mountain Formation of Utah. The site has yielded remains of symmetrodonts and triconodonts similar to those reported from the Early Cretaceous Antlers (1) and Cloverly (7) formations, respectively, of the western United States, together with tribotheres, multituberculates, and a diverse suite of well-represented lower vertebrates. Evidence from bivalves (8) and palynomorphs (9) indicates the Cedar Mountain Formation to be of middle or late Albian age; these correlations are consistent with a peak fission track determination of 101 mega-annum, based on detrital zircons from a bentonitic mudstone in the unit (10).

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Systematics of the Utah Mammal

Class Mammalia
Infraclass Tribosphenida
Supercohort Metatheria
Order and Family uncertain
Kokopellia juddi, new genus and species

Etymology. The genus is named for Kokopelli, flute-playing god of the Anasazi, and a frequent theme of petroglyphs found in the southwestern United States. The species is named for Jon Judd of Castle Dale, Utah, in recognition of his support for paleontological research in the region and for his assistance to Oklahoma Museum of Natural History (OMNH) field parties.

Type and Only Species. *Kokopellia juddi*, new species.

Holotype. OMNH 26361, left lower jaw lacking most of the ascending ramus and preserving several incisor alveoli, alveoli of C and P_1, and P_2–M_4 complete.

Locality and Horizon. OMNH locality V695, 27 km S Emery, Utah, USA; upper member, Cedar Mountain Formation (Albian; Lower Cretaceous).

Diagnosis. Similar to Cretaceous Marsupialia in postcanine dental formula and in general morphology of lower teeth but differs from all described genera in having posteriorly (rather than lingually) placed hypoconulid. Molar morphology differs from primitive tribotheres (e.g., *Kermackia*) in having relatively broader talonids and less height differential with respect to corresponding trigonids and in lacking a distal metacristid; from advanced tribotheres (e.g., *Iugomortiferum*) in having a more lingually situated paraconid and stronger labial postcingulid; and from early Eutheria (e.g., *Prokennalestes*) in dental formula, presence of a labial postcingulid, lesser development (or lack) of accessory cusps on the ultimate lower premolar, and the presence of an unreduced, more lingually situated paraconid.

OMNH 26361 preserves parts of at least two incisor alveoli, but the symphyseal region is crushed and the original number of incisors cannot be determined. Posterior to the canine, which is broken at its base, the presence of a pair of alveoli for P_1, together with all succeeding adult teeth originally present in the jaw, unambiguously establishes the postcanine dental formula as three premolars and four molars, the primitive count for marsupials (6, 11). The preserved inferior border of the dentary bone suggests that an inflected angle [a presumably primitive character retained in marsupials (11)] was present. The premolars are simple, conical cusps with small heels, lacking the antero- and posterobasal expansions seen even in the earliest eutherians (12); the last of the series, P_3, is tall [another feature of marsupials that may, or may not, be primitive (6)]. M_1 is considerably smaller than the succeeding teeth, a character common to Late Cretaceous marsupials but not generally seen among tribotheres or early eutherians. The lower molars have lingually

placed, unreduced paraconids and strong labial postcingulids, features found in early marsupials and rare or lacking among other primitive Tribosphenida (6, 11, 13), although the paraconids are not so lingually situated as they are in Campanian and later taxa. In terms of coronal pattern, the lower molars much resemble those of the typical Late Cretaceous marsupial *Alphadon*, except that the hypoconulid forms a finger-like projection and is more centrally placed at the back of the talonid, not lingually shifted and twinned with the entoconid, a diagnostic character of Marsupialia (refs. 11 and 14; Fig. 1).

Early Mammals and Marsupial Dental Characters

Few known specimens of tribosphenic mammals older than Campanian age provide direct evidence bearing on dental formula. Even with the best fossils available, establishment of homologies for postcanine teeth of nontribosphenic mammals, metatherians, and eutherians remains problematic (6, 15, 16). Despite controversies over homology, however, it is likely that either the presence in the adult of only three premolariform teeth or a combination of three premolariform and four molariform teeth represents a derived condition of marsupials within the context of Tribosphenida (6, 16). *K. juddi* possesses the marsupial dental formula and several features of lower molars hypothesized to represent marsupial synapomorphies (e.g., first lower molar considerably smaller than succeeding teeth, presence of labial postcingulid), yet lacks the most diagnostic molar specialization of the group, twinning of the hypoconulid and entoconid. Furthermore, *K. juddi* lacks any known apomorphy that would preclude it from ancestry to all known marsupials. Whether the species is included in the group or considered as simply an advanced tribothere depends on definition (13, 14); the earliest undoubted marsupials are from the Cenomanian of North America (17, 18). Nevertheless, the most parsimonious explanation for the character distribution seen in this taxon is the hypothesis that the marsupial postcanine dental formula of three premolars and four molars evolved prior to the hallmark distinguishing character of the group, the twinning of hypoconulid with entoconid. Close apposition of these cusps is hypothesized to be functionally related to an emphasis on hypocone/metacone occlusion and is accomplished differently in the eutherians that later developed the character (19). Although upper molars of *K. juddi* are not yet known, marsupials or marsupial-like species (depending on definition) from the Turonian (20) and Campanian (13) of Utah have the marsupial configuration of lower molar cusps and associated upper molar characters but lack the most distinctive specialization of upper molars—the presence of a cusp or cusps on the posterior stylar shelf (11, 14, 21)—in this respect approximating the presumed condition for more primitive tribosphenidans (6). This, in turn, suggests that evolution of a diagnostic pattern of a stylar cusp (or cusps) on upper molars appeared later than did twinning of lower molar hypoconulid and entoconid (and functionally associated dental characters) in the clade of mammals including marsupials and presumed allies; in turn, this would have been preceded by establishment of the marsupial postcanine dental formula (Fig. 2).

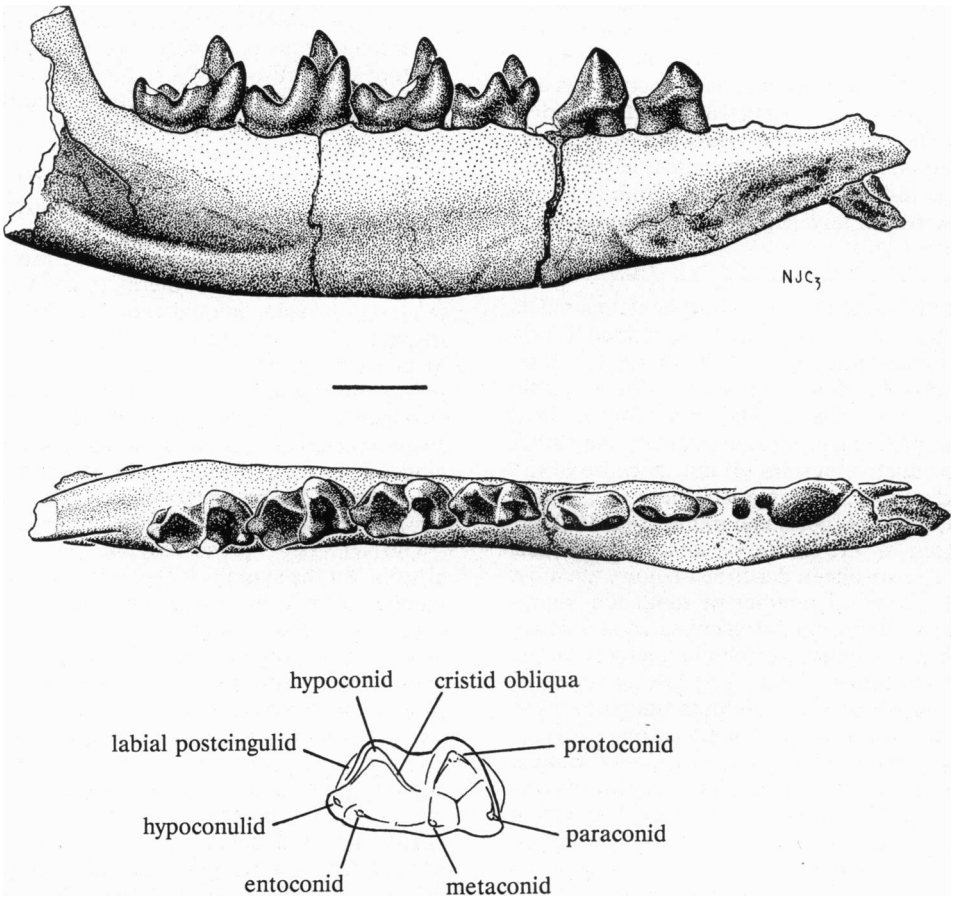

FIG. 1. *K. juddi*. Holotype mandible (OMNH 26361) in lingual and occlusal views. Bottom drawing (not to scale) shows lower molar dental terminology and morphology of a Late Cretaceous marsupial, *Alphadon* cf. *A. sahnii*, illustrating a presumed synapomorphy of the group, approximation of hypoconulid to entoconid (11, 14). The distal metacristid of primitive tribosphenic mammals, not shown here, descends posterolabially from the apex of the metaconid (5). (Bar = 2 mm.)

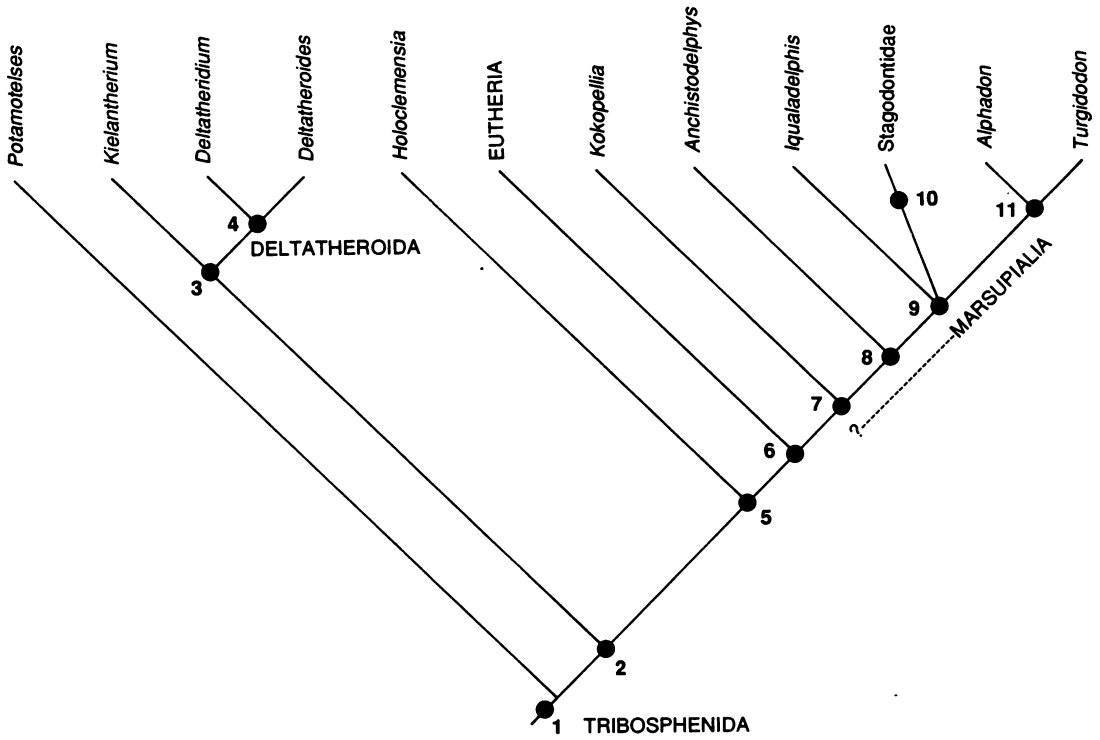

FIG. 2. Hypothesis of relationships among selected higher (tribosphenic) mammals, showing proposed sequential evolution of marsupial dental characteristics. Characters at nodes: 1, tribosphenic molars (upper molars with protocone, lower molars with fully basined, multicusped talonid); 2, upper molars with double rank prevallum–postvallid shearing (preprotocrista extends labially around base of paracone); 3, lower molars with enlarged paraconid and reduced metaconid (emphasis on postvallum–prevallid shearing; postmetacrista of upper molars assumed to be salient), M_4 reduced; 4, M_4 further reduced or lost, reduce premolar count to three (independently acquired at node 7); 5, lower molars with trigonid cusps forming acute triangle, distal metacristid lost, cristid obliqua attaches to base of trigonid; 6, upper molars with double rank postvallum–prevallid shearing (postprotocrista extends labially around base of metacone); 7, adult postcanine dental formula, three premolars and four molars (independently acquired at node 4), perhaps through nonreplacement at the locus of marsupial M_1 [eutherian P_4 (16)], lower molars with strong labial postcingulid, trigonid to talonid height differential reduced, talonid broadened, M_1 smaller than succeeding teeth (independently acquired within Deltatheroida); 8, lower molars with hypoconulid lingually placed and twinned with entoconid, ? upper molars with well-developed, labially placed, winged conules, ? upper molars with reduced height differential between paracone and metacone (upper dentition not known in *Kokopellia*); 9, paraconid of lower molars placed at extreme lingual margin of teeth (independently acquired within Deltatheroida), upper molars with cusp consistently present in D position of stylar shelf; 10, postvallum–prevallid shearing emphasized (lower molars with reduced metaconid and enlarged paraconid, upper molars with salient postmetacrista; independently acquired at node 3); 11, upper molars with cusp consistently present in C position of stylar shelf, metacone equal to or exceeding paracone in size, protocone broadened, lower molars with further reduced height differential between trigonid and talonid, talonid relatively broader. Dental terminology follows Clemens (11) and Fox (5). Characters used in diagnosing the Marsupialia (e.g., ref. 14) occur at nodes 7–9; thus, inclusion in the group of fossil taxa such as *Anchistodelphys* and *Kokopellia* depends on definition.

Phylogenetic and Biogeographic Implications

The Deltatheroida, a primitive group of higher mammals mainly Old World in distribution, has recently been forwarded as a sister group to marsupials on the basis of both dental and cranial morphology (22); the primitiveness of taxa allied to or included within Deltatheroida has further led to the suggestion that higher mammals (Tribosphenida) represent a polyphyletic assemblage (23, 24). Regardless of the position of the crown groups Marsupialia and Eutheria with respect to Deltatheroida, monophyly of Tribosphenida remains the only hypothesis corroborated by synapomorphy (Fig. 2). In terms of deltatheroidan affinities, evidence from the basicranium is difficult to evaluate because it is so poorly known for early mammals. Advanced deltatheroidans have a postcanine dental formula similar to that of marsupials [three premolars and three or four molars (25)] and resemble a North American marsupial family, Stagodontidae, in certain aspects of dental anatomy (26). However, deltatheroidans are in other respects remarkably primitive; the distribution of dental characters among marsupials, eutherians, and tribotheres suggests that the resemblances are advanced within Deltatheroida and/or Marsupialia, respectively, and therefore that they evolved independently (Fig. 2). Deltatheroidans either lack or appear to have independently acquired advanced characters shared by advanced tribotheres, marsupials, and eutherians (26). In addition, *Kielantherium*, a primitive mammal from the Early Cretaceous of Mongolia, resembles deltatheroidans (2) in certain advanced features (reduced last molars, reduced metaconid) yet retained at least four premolars (27). If *Kielantherium* is a primitive member of (or sister taxon to) Deltatheroida, this would imply that reduction to three premolars occurred independently in this group. Remaining morphologic features marshalled in support of a special relationship between deltatheroidans and marsupials (23) represent characters that are generally interpreted as plesiomorphies or whose polarity is poorly understood [relative size of talonid cusps (28); single-rooted canine, presence of four molars, relative sizes of paraconid/metaconid and paracone/metacone, morphology of last premolar (6)] or whose distribution is debatable [hypothesized loss of labial mandibular foramen, which is widely present among Cretaceous marsupials (29), among Metatheria]. Thus, in terms of dental anatomy at least, marsupials and marsupial-like mammals appear to be known only from North America prior to the end of the Cretaceous or earliest Paleocene, when they make their first appearance in the South American fossil record (30, 31). Hauterivian and

Campanian assemblages of South America record the presence of an endemic, exclusively nontribosphenic mammalian fauna (32). On this basis, a North American origin for marsupials, with latest Cretaceous dispersal to South America, has been proposed (33). The presence of a marsupial-like mammal in the Albian of North America, the diversity of marsupials on the continent by the Cenomanian (18), the sequence of dental character evolution proposed above, and the hypothesized evolution of South American and Australian taxa from a relatively advanced, *Alphadon*-like taxon (14, 34), are corroborating lines of evidence suggesting that marsupials, although highly characteristic of today's South American and Australian faunas, originated in North America.

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